THE UNIVERSITY OF ALBERTA

HELMINTHS OF CRICETIDAE WITH SPECIAL REFERENCE TO *CLETHRIONOMYS* TILESIUS, 1850.

by

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ABSTRACT

A study of the endoparasites of six cricetid rodents, with special reference to Clethrionomys spp., was carried out in northern Alberta and British Columbia and the southern District of Mackenzie in the summer of 1962 and 1963.

New host records are: Taenia rileyi and Rictularia microti from Clethrionomys gapperi and C. rutilus; Andrya macrocephala from Phenacomys intermedius; and Syphacia obvelata from Synaptomys borealis.

Hymenolepis horrida and Syphacia obvelata were the most common parasites encountered.

The parasitology of C. rutilus differed from that of C. gapperi only in that the juvenile C. rutilus were less heavily infected than were the juvenile C. gapperi.

This study indicated that parasitic infections were few in the spring but more numerous in the summer; that the incidence of parasite infection is independent of host density; and that infection with any one parasite species does not prevent subsequent infection with another parasite species.

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New host records are: *Taenia rileyi* and *Rictularia microti* from *Clethrionomys gapperi* and *C. rutilus*; *Andrya macrocephala* from *Phenacomys intermedius*; and *Syphacia obvelata* from *Synaptomys borealis*.

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ACKNOWLEDGEMENTS

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INTRODUCTION

Clethrionomys rutilus Pallas, 1779 and C. gapperi (Vigors, 1830) are closely related species of red-backed voles occurring in boreal and arctic North America. Although the ranges of the two species apparently do not overlap, the southern limits of C. rutilus and the northern limits of C. gapperi approach one another and probably meet in some areas (Fig. 1). Several theories on the origins and relationships of the two species have been presented (Hinton, 1926; Bee and Hall, 1956); but as yet definite solutions have not been found.

Parasites are often used in attempting to elucidate the evolution, taxonomy, and affinities of host groups (Metcalf, 1929; Cameron, 1950). It was hoped that an examination of the endoparasites of C. rutilus and C. gapperi would provide some insight into the relationships of their hosts. This paper is the result of such an examination.

It was decided to collect parasites from areas where the ranges of the two species of red-backed voles approached one another as well as from areas inhabited by only one species of red-back, and to collect parasites from other microtine and cricetid rodents. It was thought that such data would be useful in determining the geographic distribution and host specificity of the parasites encountered.

MATERIALS AND METHODS

The animals considered in this study were collected from mid and northern Alberta, northern British Columbia, and southern District of Mackenzie, Northwest Territories. Museum Special snap traps were used almost exclusively, but animals dying in live traps or in captivity were also examined for parasites. The traplines were checked at least twice daily - in the early morning and late evening. The animals were immediately placed in small paper bags to prevent the loss of ectoparasites. Examination for parasites was performed as soon as possible after capture. Animals taken in the morning were autopsied the same day; those taken in the late evening were examined the following morning.

A few drops of chloroform were poured into the paper bag containing the specimen to be examined. The bag was then torn open, and the ectoparasites, killed or rendered immobile by the chloroform, were collected and preserved in 70 per cent alcohol.

Sex, weight, and standard measurements were recorded for each animal as shown in Figure 2. Figure 2 also indicates the organs examined for endoparasites.

Each organ was removed and placed in water in a separate petri dish. The endoparasites were removed, washed in water, and fixed and preserved in A.F.A. (cestodes) or 70 per cent alcohol (nematodes). They were later mounted on microscope slides following standard procedures. Mayer's and especially

	No.	Location	Date
1962	1.	Mile 349.5 Alaska Highway	31 May - 1 June
	2.	Mile 374 Alaska Highway	2-14 June
	3.	Mile 403 Alaska Highway	17-21 June
	4.	Mile 340 Alaska Highway	22 June
	5.	Vega, Alberta	15-26 July
	6.	Lady Evelyn Falls, N.W.T.	3-9 August
	7.	Providence Ferry, N.W.T.	9-11 August
	8.	Stagg River, N.W.T.	13-14 August
	9.	Mosquito Creek, N.W.T.	18 August
	10.	Mile 38 Great Slave Lake Highway	19 August
	11.	Mile 66 Great Slave Lake Highway	20-21 August
	12.	Ministik Lake, Alberta	1-11 September
1963	13.	Lady Evelyn Falls, N.W.T.	4-14 July
1962	14.	Ministik Lake	16 May

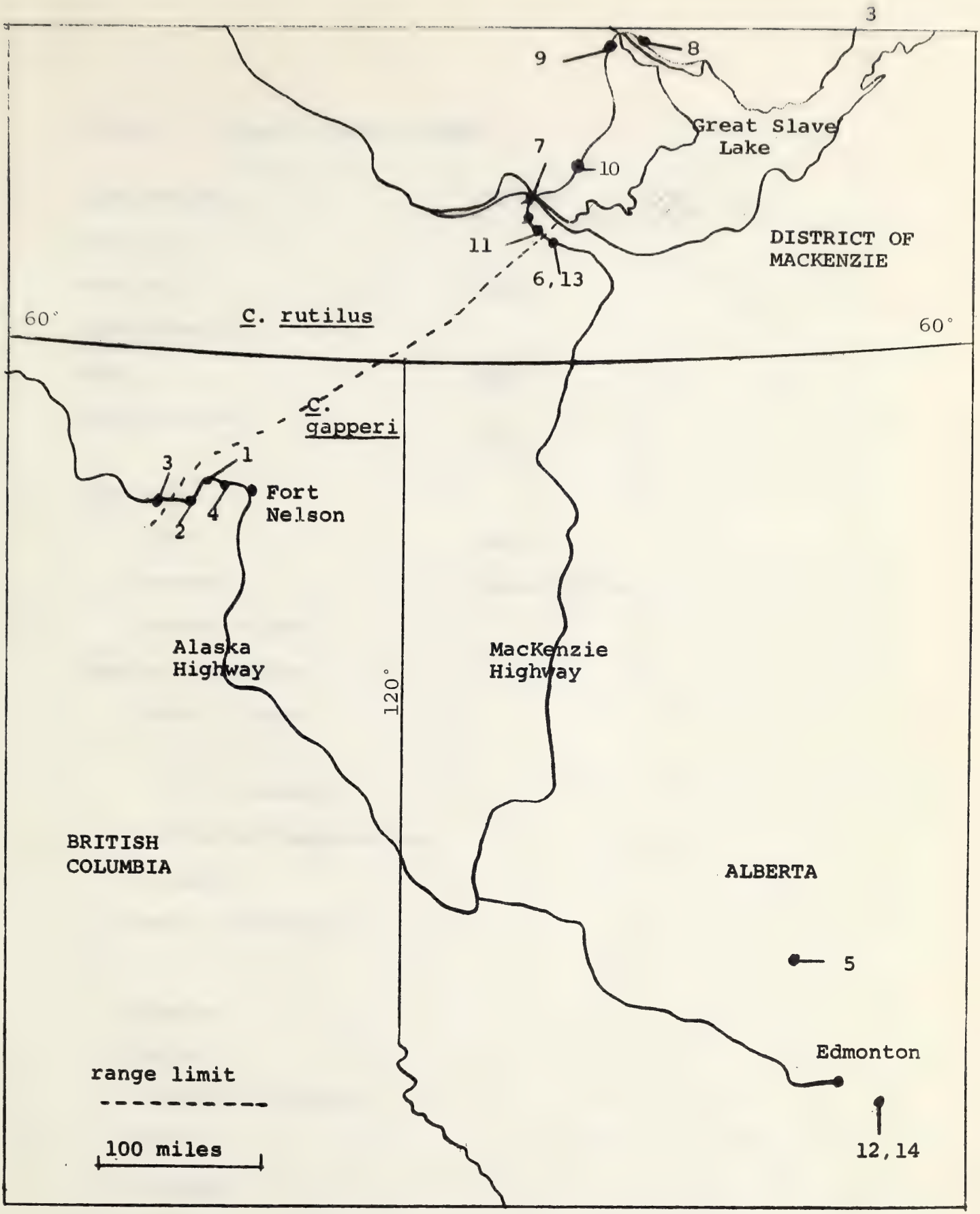


Figure 1. Map showing collection sites and approximate range limits of Clethrionomys gapperi and C. rutilus.

Figure 2. Sample autopsy sheet.

Specimen No.: Species

Locality:

Trap No.: Date:

Measurements:

Sex: Age:

Reproductive:

Specimens

Skin Skull

Stomach Reproductive

Ectoparasites

Internal Parasites

Blood: Smear

: Vessels

Coelom and mesenteries

Stomach

Small intestine

Caecum

Colon

Trachea and lungs

Liver

Pancreas

Kidney

Diaphragm

Erlich's hematoxylin were used to stain the adult cestodes after a variety of carmine stains proved unsatisfactory. The cestodes were dehydrated in increasing concentrations of alcohol, cleared in xylene and mounted in Canada balsam.

Larval cestodes were preserved in A.F.A. and examined in the laboratory. The cysts of larval cestodes were dissected in water with fine needles, and the scolex, when present, was placed on a glass slide in a drop of water and teased to free the hooks. The hooks were then permanently mounted in Aquamount.

Measurements of the hooks were made as suggested by Stevenson and Engberg (1904), and using a camera lucida. This allowed comparisons with the data presented by Riser (1956).

Ectoparasites were removed from the alcohol, washed in water, and mounted in Aquamount.

Nematodes were not stained, since they were small in size and clearing revealed their internal structures. Various methods were tried in preparing whole mounts of nematodes. First, they were dehydrated in alcohols, cleared in xylene, cedarwood oil, oil of cloves, or other organic agents, and mounted in Canada balsam. Specimens treated in the above manner were often ruined by the penetration of air. This penetration most frequently occurred during the transfer of the nematodes from clearing agent to balsam, but occasionally mounted specimens became air-filled some days after preparation. Shrinkage and distortion caused by too rapid penetration of of the organic clearing agents occurred in many of the speci-

mens so prepared.

A more satisfactory method was that described by Basir (1949). The nematodes were transferred from 70 per cent alcohol to glycerine alcohol (5 parts 70 per cent alcohol, 25 parts glycerine) and the alcohol was allowed to evaporate, leaving the nematodes in pure glycerine, by which agent they were cleared. The worms were then mounted in liquid glycerine jelly, a coverslip was applied, and the glycerine jelly was allowed to solidify. Air did not enter any of the specimens so prepared. An added advantage of the above method was that the worms could be "unmounted". This is, the solid glycerine jelly could be melted, and the worm moved to expose a partially concealed structure, or removed completely and stored in glycerine alcohol. En face views of nematodes were prepared as described by Basir (1949).

Various keys proved useful in identifying the endoparasites to the family or generic level. Among these were Yamaguti (1959, 1961), Spassky (1961), Skrjabin et al. (1961), and Wardle and McLeod (1952). Considerable disagreement existed among these authorities and no one key was completely reliable. For specific identification it was necessary to consult original descriptions or revisions. Representative specimens are deposited with the United States National Museum and the Department of Zoology, University of Alberta.

Host identifications were made by Dr. W. A. Fuller, Department of Zoology, University of Alberta and study skins and skulls of host species are deposited in that Department.

Drawings were made with the aid of a camera lucida.

RESULTS

Autopsies were performed on 423 small mammals. Table I records the number of each host species examined, together with the percentage infection of each species. Three specimens of the genus Clethrionomys which could not be specifically identified were infected with parasites (Table I).

Table II summarizes the results in terms of host-parasite relationships.

Table III presents data on the areas in which investigations were carried out, and records the species of parasite infecting each host in each area.

Table IV combines my data with host-parasite records from the literature.

Table I. Per cent of hosts infected with one or more endoparasitic species.

Host	No. Autopsied	% Parasitized
Clethrionomys gapperi	168	48
C. rutilus	147	23
C. sp.	3	100
Microtus pennsylvanicus	35	26
Phenacomys intermedius	12	33
Synaptomys borealis	4	25
Peromyscus maniculatus	54	7
Total	423	32

Table II. Per cent of hosts infected with each parasite. Numbers in parentheses represent average intensity of infection.

Parasite / Host	Clethrionomys gapperi	C. rutilus	Microtus pennsylvanicus	Phenacomys intermedius	Synaptomys borealis	Peromyscus maniculatus
Andrya macrocephala	4(2)	1(1)	3(3)	33(1)		
Paranoplocephala variabilis			9(1)			
Catenotaenia dendritica	2(1)					
Hymenolepis horrida	32(3)	16 (2)	3(1)			
Taenia mustelae	2					
T. rileyi	1	3				
Paruterina candelabraria						2
Capillaria hepatica						4
Protospirura muris	1(2)	1 (2)				
Rictularia microti	1(3)	5 (3)				
Syphacia obvelata	16(25+)	3 (25+)				
Unident. larval cestodes	8	5	11			
Unident. larval acanthocephalan						4(1)

Table III. Number of hosts infected with each parasite at each location.

Host	*Clethrionomys gapperi*							*C. rutilus*						*C. sp.*		*Microtus pennsylvanicus*								*Phenacomys intermedius*				*Synaptomys borealis*		*Peromyscus maniculatus*					
Location	1	2	4	5	6	12	13	3	7	8	9	10	11	6	11	1	2	3	4	6	8	12	13	2	3	6	13	6	13	1	2	3	4	12	14
No. Examined	3	16	3	16	64	49	17	6	33	15	39	11	42	2	1	4	6	3	2	8	2	3	7	1	1	4	6	1	3	3	18	26	1	1	5
Parasite:																																			
Cestoda																																			
Andrya macrocephala		1		1		4	1						1										1			1	3								
Catenotaenia dendritica				2		1																													
Hymenolepis horrida			1	3	28	15	8		11	3	9			2									1												
Paranoplocephala variabilis																1	1		1																
Paruterina candelabraria																															1				
Taenia mustelae					3																														
T. rileyi					2								4																						
Unid. larval cestodes			1		2	5	2	1	1				1			2		2																	
Nematoda																																			
Capillaria hepatica																																			2
Protospirura muris			1		1				1																										
Rictularia microti					1				2				5		1																				
Syphacia obvelata					9	12	5		3	1																			1						
Acanthocephala																																			
Unid. larval acanthocephalan																																			2

Note: see Fig. 1 for Location code and date.

Table IV. Endoparasites of hosts considered in this study and host-parasite records from the literature.

Parasite	Host						
	Clethrionomys gapperi (Vigors, 1830)	C. rutilus Pallas, 1779	Microtus pennsylvanicus (Ord, 1815)	Phenacomys intermedius Merrian, 1889	Synaptomys borealis (Richardson 1828)	Microtus spp.	Phenacomys spp.
CESTODA Andrya arctica Rausch, 1952		Rausch, 1952b			Lubinsky, 1957	(1) Rausch, 1952b	
A. biardi, Schad, 1954						(1) Schad, 1954	
A. macrocephala Douthitt, 1915	Murray, 1964	Murray, 1964	Murray, 1964	*Murray, 1964		(7) Schad, 1954	
A. primordialis Douthitt, 1915	Lubinsky, 1957		Lubinsky, 1957	Lubinsky, 1957		(3) Rausch & Schiller, 1949b	
A. spp.			Rausch and Tiner, 1949			(1) Kuns and Rausch, 1950	(1) Voge, 1955
Paranoplocephala infrequens (Douthitt, 1915)			Lubinsky, 1957		Schad, 1954	(7) Rausch 1952b	
P. spp.			Rausch and Tiner, 1949			Rausch and Tiner, 1949	
Hymenolepis horrida (von Linstow, 1901)	Murray, 1964	Murray, 1964	Murray, 1964			(6) Schiller, 1952	
H. evaginata Barker and Andrews, 1915			Rausch and Tiner, 1949				
H. fraterna Stiles, 1915			Rausch and Tiner, 1949				
H. spp.			Rausch and Tiner, 1949				
Catenotaenia dendritica (Goeze, 1782)	Murray, 1964	Rausch, 1957					
Echinococcus multilocularis Leuckart, 1863		Rausch, 1957	Rausch and Schiller, 1956 (exp.)			(3) Rausch & Schiller, 1956 (2 exp.)	

cont'd....

Table IV. (cont'd...)

Parasite	Host						
	Clethrionomys gapperi	C. rutilus	Microtus pennsylvanicus	Phenacomys intermedius	Synaptomys borealis	Microtus spp.	Phenacomys spp.
Cladotaenia globifera (Batsch, 1786)	Freeman, 1959						
C. mirsoevi Skrjabin and Popoff, 1924	Lubinsky, 1957						
Paruterina candelabraria (Goeze, 1782)	Freeman, 1957 (exp.)						
Taenia mustelae Gmelin, 1790	Murray, 1964	Rausch, 1957	Lubinsky, 1957	Schad, 1954		(3) Lubinsky 1957	
T. rileyi Loewen, 1929	*Murray, 1964	*Murray, 1964					
T. taeniaeformis (Batsch, 1786)			Rausch and Tiner, 1949				
T. spp.			Rausch and Tiner, 1949				
NEMATODA							
Capillaria hepatica (Bancroft, 1893)							
C. muris-sylvatica (Diesing, 1851)			Rausch and Tiner, 1949				
C. spp.		Rausch, 1952b					
Dictyocaulus viviparus (Bloch, 1782)			Rausch and Tiner, 1949				
Heligmosomoides polygyrus (Dujardin, 1845)				Lubinsky, 1957			
Heligmosomum spp.			Erickson, 1938				
Longistriata dalyrymplei Dikmans, 1935			Rausch and Tiner, 1949				

cont'd....

Table IV. (cont'd....)

Parasite	Host						
	Clethrionomys gapperi	C. rutilus	Microtus pennsylvanicus	Phenacomys intermedius	Synaptomys borealis	Microtus spp.	Phenacomys spp.
Nematospira turgida Walton, 1923			Walton, 1923				
Nematospiroides longispiculatus Dikmans, 1940			Dikmans, 1940				
N. spp.		Rausch, 1957	Rausch and Tiner, 1949				
Protospirura muris (Zimmermann, 1780)	Murray, 1964	Murray, 1964	Rausch and Tiner, 1949				
Rictularia coloradensis Hall, 1916			Lubinsky, 1957			(1) Rankin, 1945	
R. microti McPherson & Tiner, 1952	*Murray, 1964	*Murray 1964				(2) McPherson & Tiner, 1952	
R. spp.						(1) Rausch, 1952b	
Syphacia obvelata (Rudolphi, 1802)	Murray, 1964	Murray, 1964	Schad, 1954		*Murray, 1964	(3) Kuns and Rausch, 1950	
Trichurus opaca Barker and Noyes, 1915			Kuns and Rausch, 1950				
TREMATODA							
Brachyliana spp.			Rausch, 1952b				
Entosiphonus thompsoni Sinitsin, 1931			Rausch and Tiner, 1949				
Mediogonomus ovilacus Woodhead and Malewitz, 1936			Rausch and Tiner, 1949				
Plagiorchis muris Tanabe 1922			Schad, 1954				
Plagiorchis spp.	Schad, 1954	Rausch, 1952b					

cont'd....

Table IV. (cont'd....)

Parasite	Host						
	Clethrionomys gapperi	C. rutilus	Microtus pennsylvanicus	Phenacomys intermedius	Synaptomys borealis	Microtus spp.	Phenacomys spp.
Quinquiserialis hassalli (McIntosh & McIntosh, 1934)			McIntosh and McIntosh, 1934				
Q. hassalli (Barker and Laughlin, 1911)			Schad, 1954				
ACANTHOCEPHALA Unidentified larvae							

Parasite	Host							
	Synaptomys	Other Microtines	Peromyscus maniculatus	Other Cricetines	Muridae	Geomyidae	Heteromyidae	Sciuridae
CESTODA:								
Andrya arctica		(2) Rausch, 1952b						
A. biardi								
A. macrocephala		(1) Rausch, 1952b		(1) Voge, 1955		(2) Rausch & Schiller, 1949b		(1) Rausch, 1952b
A. primordialis				(1) Voge, 1955				(1) Douthitt, 1915
A. sp.	(1) Erickson, 1938							
Paranoplocephala infrequens						(1) Douthitt, 1915		
P. spp.	(1) Rausch, 1952b	(1) Schad, 1954				(1) Lubinsky, 1957		
Hymenolepis horrida								
H. evaginata	(1) Rausch 1950		(3) Voge, 1952				(1) Voge, 1952	
H. fraterna								
H. spp.								
Catenotaenia dendritica		(1) Smith, 1954		(1) Voge, 1955		(1) McIntosh, 1941	(5) Voge, 1949	(2) Rausch & Tiner, 1948
Echinococcus multilocularis		(1) Rausch, 1957						
Cladotaenia globifera								

cont'd....

Table IV. (cont'd....)

Parasites	Host							
	Synaptomys	Other Microtines	Peromyscus maniculatus	Other Cricetines	Muridae	Geomyidae	Sciuridae	Aplodontiidae
C. mirsoevi								
Paruterina candelabraria								
Taenia mustelae	(1) Freeman, 1956	(3) Rausch, 1957		(3) Freeman, 1956		(1) Lubinsky, 1957	(4) Freeman, 1956	(1) Locker, 1955
T. rileyi		(1) Rausch, 1952a		(3) Riser, 1956			+(1) Holmes, 1964	
NEMATODA Capillaria hepatica			Murray, 1964					
Protospirura muris				(1) Schad, 1954				
Rictularia coloradensis				(1) Tiner, 1948			(4) Grundmunn, 1957	
R. spp.				(1) Grundmann, 1957			(4) Rausch & Tiner, 1948	
Syphacia obvelata				(3) Hall, 1916	(2) Rausch & Tiner, 1949			
ACANTHOCEPHALA Unidentified larva			Murray, 1964					

Notes:
1. The numbers in parentheses indicate the number of host species from which the parasite has been reported.
2. Only the latest author is recorded.
3. * - new host record.
4. exp. - experimental infection.
5. + - personal communication

PARASITES ENCOUNTERED

Rausch (1951) states "In various anoplocephaline genera, ... the lack of constant morphological characters (e.g. rostellar hooks) makes it necessary to pay particular attention to variation when specific determination is attempted." Variability in state of contraction of specimens results in apparent differences in organ size and distribution which do not, in fact, exist. The literature contains many descriptions of anoplocephaline species which were invalidated when adequate series, which exposed these new species as variants of an already described species, became available. The same is true to a lesser extent of some of the nematode parasites.

It seems pertinent here to present a brief review of the taxonomic status of the helminths herein considered, and to present the reasons for their identification, since agreement on species assignations are not always unanimous in the literature.

Cestoda

The Genus Andrya Railliet, 1883

Ten species of the genus Andrya have been described from rodents of North America. Only six species, four of which occur in microtine rodents, are generally recognized as valid. These are: Andrya primordialis Douthitt, 1915; A. macrocephala Douthitt, 1915; A. arctica Rausch, 1952; A. bairdi Schad, 1954; A. neotomae, Voge, 1946; and A. sciuri Rausch, 1947.

Andrya primordialis, the only North American species having a prostate gland, was described by Douthitt (1915) from Tamiasciurus hudsonicus Erxleben, 1777. At the same time, from Clethrionomys gapperi (Vigors, 1830), he described another species, also with a prostate gland, which he called A. communis. Douthitt admitted that many of the differences between the two species were probably due to differences in the state of contraction in the material, and both species were described from fragmented material. Baer (1927) regarded the two names as synonyms - and A. primordialis was retained because of priority. Later writers have accepted this synonomy, but Lubinsky (1957) reported A. communis from Microtus pennsylvanicus (Ord, 1815) in Alberta.

The genus was separated by Kirschenblatt (1938) into two subgenera - Andrya and Aprostatandrya - depending on the presence or absence of a pedunculated prostate gland. Spassky (1961) gave these subgenera full generic status. Rausch (1952b) re-examined Douthitt's material and was unable to find the prostate. Thus the uncertain status of North American cestodes possessing the prostate gland make it preferable to use the older nomenclature.

Douthitt (1915) described A. macrocephala from Geomys bursarius (Shaw, 1800). No new North American species were reported until 1946, when Voge described A. neotomae from Neotoma fuscipes Baird, 1858. A. microti Hansen, 1947, was described from Microtus pennsylvanicus, and A. sciuri Rausch 1947 and A. ondatrae Rausch, 1948, from Glaucomys sabrinus (Shaw, 1801) and Ondatra zibethica (Linnaeus, 1758) respectively. At this time the number and

distribution of the testes and diameter of the ventral excretory canal had been regarded as being of primary importance in species determination. Rausch and Schiller (1949b) examined a large quantity of Andrya material and concluded that A. microti and A. ondatrae were synonyms of A. macrocephala, and, further, that testes number and ventral excretory canal diameter are not as reliable taxonomic characters as had been supposed. Scolex size, strobila size, and sucker development were found to be of little value in separating the species of Andrya. Variation in the above characters had no relation to host species. The most reliable characters appeared to be average egg size and testes distribution, combined with size of cirrus sac.

The characters by which the then-recognized species of Andrya could be differentiated are recorded in the following key, adapted from Rausch and Schiller, 1949b.

1. Prostate gland present; unilateral genital pores. A. primordialis.
2. Prostate gland absent; irregularly alternating genital pores.
   - A. Average egg diameter 33μ (range: 26-43μ); testes usually overlap longitudinal excretory canals on one side only; ventral excretory canals may be much enlarged. A. macrocephala.
   - B. Cirrus sac 320-444μ long; testes confined to area within longitudinal excretory canals; average egg diameter 53μ. A. neotomae.
   - C. Cirrus sac 200 x 85μ; egg diameter 52-56μ. A. sciuri.

It should be noted that relatively few specimens of A. neotomae and A. sciuri were available and that variation in the characters regarded as being of specific importance may be greater than is indicated here.

Rausch (1952b), on examining specimens of A. macrocephala from New York west to California and Washington and from Mexico City north to central Alaska and St. Lawrence Island, extended the egg size limits (36 x 27μ - 51 x 41μ). He concluded that great variation in egg size and shape (ovoid to spherical) must be accepted and that there is no recognized correlation between morphological variation in A. macrocephala and host species occurrence.

In the same paper Rausch described a new species of Andrya, without a prostate gland, A. arctica. This cestode was differentiated from A. macrocephala by its larger cirrus sac (194 to 352μ long by 57 to 136μ wide) and by its larger egg size, averaging about 65 x 50μ. The genital pores were irregularly alternate.

Rausch (1952b) also had in his possession specimens of the genus Andrya which were not assigned to a species. Although lacking a prostate gland and possessing alternating genital pores, these specimens seemed close to A. primordialis in egg size and testes distribution. Rausch suggested they might also be immature or aberrant specimens of A. macrocephala.

A. bairdi Schad, 1954 was described from Microtus crotorhinus (Miller, 1895). It is characterized by having unilateral

genital pores and no prostate gland. The testes are confined to the area between the longitudinal ducts.

Schad (1954) also had in his possession specimens from "red backed mice", (C. gapperi) which lacked the prostate gland, had unilateral genital pores, and whose testes were not confined to the area between the longitudinal excretory ducts. He suggests the possibility that all North American Andrya possessing unilateral genital pores may be proved to be conspecific when an adequate series of specimens becomes available. This would require the redefinition of A. primordialis, and this has not yet been accomplished.

Andrya macrocephala Douthitt, 1915

All of the specimens of the genus Andrya recovered in this study have been assigned to the species macrocephala. None possessed a prostate gland, and no specimen with unilateral genital pores was found. Egg size and shape were variable; ranging from 23 x 28μ to 51 x 51μ in size, and from spherical to ovoid in shape. These measurements exceed the limits established by Rausch (1952b) (see above p.20). Size of cirrus sac ranged from 111 x 46μ to 231 x 65μ. The testes usually overlapped the longitudinal excretory canals on the aporal side of the segment, but in one specimen, the testes were situated entirely within the canals. Degree of contraction of the specimen strongly affects such characters as cirrus sac size and position of testes. The cirrus sac was small, and the testes within the longitudinal excretory canals

in a partially contracted specimen. The suckers of the scolex were variable in shape and degree of contraction. Figs. 3, 4 and 5 depict representative segments and scolices of A. macrocephala taken in the course of this investigation.

My material sheds no light on the taxonomic status of Andrya spp. not possessing a prostate gland but having unilateral genital pores, and whose testes are not confined to the areas between the longitudinal excretory ducts. None of my specimens had unilateral genital pores, but one specimen approaching this condition was taken from C. gapperi at Lady Evelyn Falls in 1963.

Life Cycle. The intermediate hosts of the genus Andrya are soil dwelling mites of the superfamily Oribatoidea. (Spassky, 1961)

Geographic Distribution. A. macrocephala is probably holarctic in distribution. Rausch and Schiller (1949b) suggested that A. macrocephala was conspecific with the old world species A. caucasica Kirschenblatt, 1938. Spassky, Romanova, and Naidinova (1951) concluded that A. caucasica and A. bialowizensis Soltys, 1949 are either conspecific with A. macrocephala, or that the latter, if a distinct new world species, is morphologically indistinguishable from the former two.

In North America, A. macrocephala has been reported from several areas of western United States and western Canada, Alaska, and St. Lawrence Island. Records are few in central and eastern North America, but this parasite has been found

in North Carolina, New York, and Quebec. Patterns of geographic distribution obtained from the literature are often incomplete due to lack of investigation in many areas. This may account for the apparent rarity of A. macrocephala in central North America.

Host Occurrence. Although A. macrocephala, from host records, appears to be primarily a parasite of microtines, it has been reported from a number of families (Table IV) and thus is not limited to microtine or even cricetid rodents. Host records suggest that A. macrocephala is more important as a parasite of Microtus spp. than of other microtine genera. This, I think, is because the parasite fauna of Microtus spp. is better known than that of the other microtines. I found A. macrocephala in Microtus pennsylvanicus, Clethrionomys rutilus, C. gapperi, and Phenacomys intermedius Merriam, 1889. Of these, P. intermedius is a new host record.

The Genus Paranoplocephala Luhe, 1910

Eight species of the genus Paranoplocephala, six of which are now considered valid, have been described from North American rodents. These are: P. omphalodes (Hermann, 1783); P. variabilis (Douthitt, 1915); P. infrequens (Douthitt, 1915). P. neofibrinus, Rausch, 1952; P. lemmi, Rausch, 1952; and P. wigginsi Rausch, 1954.

Baer (1927) considered P. infrequens and P. variabilis to be conspecific, but Rausch and Schiller (1949a) found

that P. infrequens had been incorrectly characterized, and that the two species, as described by Douthitt, were morphologically distinct. At the same time, they raised Douthitt's variety P. variabilis borealis to full specific rank - P. borealis (Douthitt, 1915). Rausch, 1952b, after studying a good series of P. borealis and P. variabilis, decided that the two were in fact synonomyous and the name P. variabilis was retained. P. troeschi Rausch, 1946 was described from Microtus pennsylvanicus but was found to be a synonym of P. infrequens (Rausch and Schiller, 1949a); P. kirbyi Voge, 1948, was described from Microtus californicus (Peale, 1848). Rausch (1952b) pointed out that this was a case of misidentification, and that the cestode described by Voge was actually Andrya macrocephala.

P. neofibrinus Rausch, 1952a was described from Neofiber alleni True, 1884 and P. wigginsi Rausch, 1954 from Citellus undulatus barrowensis (Merriam, 1900). These species have not been found in microtine rodents.

P. omphalodes (Hermann, 1783) was first authoritatively reported from North America by Rausch (1952b). In the same paper, P. lemmi was described.

As with Andrya, the species of Paranoplocephala are highly variable, and intraspecific variation has not been shown to correspond with geographical location or host occurrence.

Each of the species infecting microtine rodents does have, however, some distinctive characters and those used to identify

the species of Paranoplocephala encountered in this study are included in the following table compiled from the literature.

Table V. Diagnostic characteristics of Paranoplocephala spp.

Species	Habitat	Length of Strobila	Testes Distribution
P. infrequens	caecum	4 - 11.5 mm	do not extend beyond ventral longitudinal excretory canal
P. variabilis	s. intestine	5 - 15 mm	do extend beyond ventral longitudinal excretory canal
P. lemmi	caecum	10 - 20 mm	
P. omphalodes	s. intestine	150 - 195 mm	

Paranoplocephala variabilis (Douthitt, 1915)

The Paranoplocephala examined were all less than 15 mm in length, were recovered from the small intestine of the host, and had testes extending beyond the ventral longitudinal excretory canal. They were therefore identified as P. variabilis. Typical scolices and proglottids are shown in Figs. 6 and 7.

Life Cycle. The intermediate hosts of the genus Paranoplocephala are soil dwelling mites of the superfamily Oribatoidea (Spassky, 1961).

Geographic Distribution. P. variabilis, like A. macrocephala is widely distributed in North America, ranging from Alaska southward at least to the Lake States and east to Labrador. Again, records in central North America are lacking. This species is not known from Asia, but at least one Eurasian species (Spassky, 1961) resembles P. variabilis in several respects. It may, then, be holarctic in distribution.

Host Occurrence. Table IV indicates that P. variabilis is almost exclusively a parasite of microtine rodents in general, and of Microtus spp. in particular. To my knowledge, it has never been reported from Clethrionomys spp., but it has been found in the Geomyidae. This may be an accidental occurrence since it is the only report from non-microtines. P. variabilis then seems to be more host specific than A. macrocephala. I found P. variabilis only in M. pennsylvanicus.

The Genus Catenotaenia Janicki, 1904

There is no agreement as to the number of species of this genus found in North America rodents, but at least three species appear to be valid. These are: C. dendritica (Goeze, 1782) C. californica Dowell, 1953 and C. reggiae Rausch, 1951.

C. linsdalei McIntosh, 1941, was declared synonymous with C. dendritica by Schad (1954) and Smith (1954) independently. Voge (1955) suggests that C. californica may be conspecific with C. dendritica, but Wolfgang (1956) maintains the validity of the former species, agreeing with Dowell that

the lack of a dorsal excretory canal in his specimens is a constant and reliable character for specific determination.

Smith (1954) described C. peromysci and C. laguri from P. maniculatus (Wagner, 1845) and L. curtatus (Cope, 1868). Wolfgang argues that both C. laguri and C. peromysci are synonymous with C. dendritica. One of the characters that has been used to separate species of the genus is the relative arrangement of organs - in particular whether or not the testes lie in one field behind the ovary or are divided by the longitudinal uterus. Wolfgang feels that too much emphasis has been placed on testes distribution, suggesting that the size and the development of the uterus determine their position, and that pressure applied to the strobila in fixing or mounting may displace the testes to either side of the uterine stem. Wolfgang (1956) and Rausch (1951) agree that the gravid segment (i.e. the gravid uterus) "may show specific features more readily recognized than those seen in mature segments alone." In particular, they refer to the number of primary uterine branches, which, in combination with other characters, serves to separate the species of the genus Catenotaenia.

If one accepts the conclusions of Wolfgang, there remain three valid species of Catenotaenia in North America. Unfortunately these cannot be separated by uterine branching since C. dendritica (if we accept the synonomy of C. linsdalei, C. peromysci and C. laguri) has 25-50 uterine branches, C. reggiae, 30 to 40, and C. californica 25-30. C. reggiae, however, is

distinct because of its great length (360 mm) and its large number of testes (360). C. dendritica is 30-164 mm long with fewer than 200 testes (90-190), while C. californica is about 82 mm in length and has 72-90 testes. C. californica and C. dendritica may presumably be separated by the lack of the dorsal excretory canal in C. californica and by the number of testes.

It should perhaps be mentioned that Wolfgang had not actually seen Smith's material before invalidating C. peromysci and C. laguri, and that the discrepancies he cites between the measurements in the text and those taken from Smith's drawings may be due to the process of reproducing the drawings. Wolfgang himself errs when he gives the number of primary uterine branches of C. reggiae as "15-20x2", since Rausch (1951) clearly states in his description "... gravid uterus ... with 30 to 40 lateral branches ... on each side". However, Wolfgang has made the most thorough study of the genus to date, and I feel that his judgement should be accepted.

Catenotaenia dendritica (Goeze, 1782)

Only three specimens of the genus Catenotaenia were recovered in this study, and in each case only mature and gravid segments were found. In one instance, the fragments were in the caecum of the host, rather than the small intestine. The fragments were recognized as belonging to the genus Catenotaenia because of the taeniid nature of the uterus.

There were about 100 testes in each specimen, and the gravid uterus had 25-30 primary uterine branches. The specimens were assigned to the species C. dendritica. Typical segments are illustrated in Figs. 8 and 9.

Life Cycle. The intermediate hosts of the genus Cateno-taenia are tyroglyphid mites (Spassky, 1961).

Geographic Distribution. C. dendritica is cosmopolitan in distribution, having been reported from Sciurus spp.in Eurasia and in Africa, as well as from various parts of North America. As with A. macrocephala and P. variabilis the distribution of C. dendritica in North America is widespread but spotty, and seems to correspond with the areas in which fairly thorough investigation has been carried out. In western North America, it ranges from Alaska south to California and New Mexico. It has been reported from the Lake States, and from Quebec in eastern Canada.

Host Occurrence. C. dendritica has been reported from several rodent families (Table IV), but its occurrence in microtines is not widespread. To my knowledge, it has been found only in C. rutilus, C. gapperi and Lagurus curtatus. It is possible that this parasite is accidental in occurrence in microtines, although Schad (1954) found it to be "the commoner tapeworm of red-backed mice" in Quebec and Labrador. Rausch (1952b)states that "with possible local exceptions, it is not a common parasite in North American microtine rodents". I found C. dendritica only in C. gapperi.

The Genus Hymenolepis Weinland, 1858

Hughes (1941) has presented a key to more than 300 known, and, at the time, supposedly valid species of Hymenolepis. The rodents of North America are infected with several species of Hymenolepis, most of which are provided with an armed rostellum. All of the Hymenolepis specimens encountered in this study lacked the rostellum, and have been identified as H. horrida (von Linstow, 1901).

Hymenolepis horrida (von Linstow, 1901)

H. horrida was first reported from North America by Kuns and Rausch (1950); but because of its prevalence, it must certainly have been collected and misidentified prior to this time.

Species of the genus Hymenolepis have been found to be highly variable (Voge, 1952; Freeman, 1960; Schiller, 1952, 1959a b, c, d) and H. horrida is perhaps the most variable of all. Schiller (1952) has presented a study dealing with morphological variation in H. horrida that resulted in the broadening of the species concept. He found that with the possible exception of cirrus spine size and cirrus sac diameter, variation in any one character appeared to be completely independent of variation in any other character. Typical specimens collected in this study, exhibiting morphological variation, are represented in Figs. 10-13.

Life Cycle. The intermediate hosts of the genus Hymeno-

lepis are a wide variety of arthropods (Schiller, 1952).

Geographical Distribution. H. horrida is holarctic in distribution and was well known from Eurasia before its recovery from North America. Its distribution in North America seems to correspond with the boreal forest. South of the boreal forest, it appears to be rare, "occurring mainly in voles from subalpine or alpine habitats" (Rausch, 1952b). It has been reported from Alaska south to California, in Quebec in eastern Canada, and in the state of Tennessee.

Host Occurrence. Host records indicate that H. horrida is primarily a parasite of microtine rodents, although it has been reported from cricetines and from other rodent families (Table IV).

My work suggests that H. horrida is more important as a parasite of Clethrionomys spp. than of Microtus pennsylvanicus. It is possible that ecological specificity rather than host specificity is in operation here. This point will be more fully discussed in comparing the parasitic fauna of Clethrionomys spp. and M. pennsylvanicus. I recovered H. horrida from C. rutilus, C. gapperi and M. pennsylvanicus.

The Genus Taenia Linnaeus, 1758.

Several species of the genus Taenia have been recorded as larvae from North American rodents. Without exception, these species are adult in carnivorous mammals. The species can usually be identified by the morphology of their rostellar

hooks. At least two species, T. rileyi Loewen, 1929 and T. mustelae Gmelin, 1790, were encountered in the present study.

Taenia rileyi Loewen, 1929

This species has had a confused taxonomic history and many instances of misidentification have undoubtedly occurred. Riser (1956) revealed that Loewen's original description of this species is a composite, the strobila being new, but the scolex being that of T. laticollis Rudolphi, 1819. The situation was further obscured by the description of T. lyncis Skinker, 1935. This species was described from the strobila of T. omissa Lühe, 1910 and the scolex of T. rileyi. The larval stages of T. rileyi would then have been identified as T. laticollis from 1929 to 1935 and as T. lyncis from 1935 to 1956.

The hooks of T. rileyi examined in this study were in some cases slightly larger in all dimensions than the measurements of Riser.

Table VI. Hook measurements of T. rileyi.

		Total length (mm)	Handle (b) (mm)	Blade (c) (mm)
Riser 1956	Large	0.22 - 0.24	0.17 - 0.18	0.10 - 0.11
	Small	0.16 - 0.17	0.11	0.07
Murray 1964	Large	0.21 - 0.25	0.17	0.11 - 0.12
	Small	0.15 - 0.19	0.12 - 0.14	0.08 - 0.09

Several factors may be involved here. First of all, a difference in technique in teasing and orientation of the hooks could have contributed to discrepancies in the measurements. Sometimes it is difficult to determine whether a hook is in full lateral or slightly rotated view. Slight rotations can cause appreciable change in the size of the dimensions. Secondly, Riser's material came from Utah and California; mine from Alberta and the N.W.T. Geographical variation in size of hooks may account for the larger size of my hooks. On examining van Zyll's (1963) T. rileyi material from Alberta lynx, I found that the dimensions of some of the hooks were slightly larger than those reported by Riser.

In any case, camera lucida images of my hooks could be exactly super-imposed on Riser's drawings of T. rileyi hooks, thus leaving no doubt of their identity (Fig. 14).

Life Cycle. Although T. rileyi has been once reported from Canis latrans Say, 1823 in Minnesota, its most important final host is the lynx, Felis lynx Linnaeus, 1758. Its larval stage occurs in small rodents.

Geographic Distribution. The geographic distribution of T. rileyi must conform with that of its final hosts. It is known in the adult form from Alberta, Minnesota, and California. In the larval stage it has been reported positively from the above areas, and has been tentatively identified from North Carolina, Georgia, and Florida (Harkema and Kartman, 1948; Rausch, 1952a). It is probably widespread throughout North America, but the confused state of its taxonomy up to 1956

would perhaps have prevented its proper recognition. This species, to my knowledge, has not been reported from Eurasia.

Host Occurrence. Few records of T. rileyi appear in the literature and definite conclusions as to its host specificity cannot be drawn. It is adult in carnivorous mammals, primarily in felids. Its certain intermediate hosts are Peromyscus maniculatus, Tamiasciurus hudsonicus, Clethrionomys gapperi, and C. rutilus. Tentatively, it has been reported from Sigmodon hispidus Say and Ord, 1825, and Neofiber alleni. It probably infects a large number of rodents preyed upon by the definitive hosts. My recovery of this species from C. gapperi and C. rutilus apparently constitute new records.

Taenia mustelae Gmelin, 1790

The taxonomic status of T. mustelae was clarified and defined by Freeman (1956). The larval hooks, when fully developed, have an unmistakeably characteristic shape. The hooks examined by me conformed both in size and shape to those described and depicted by Freeman. They are presented in Fig. 15. Before 1956, the taxonomy of this species was somewhat poorly defined, and many larval T. mustelae were misidentified as Cladotaenia sp. Both uni- and multi-scolex larvae are produced by this tapeworm, sometimes in the same host. Both types were encountered in the present study, but never in the same host.

Life Cycle. The adult cestode is found in mustelid mammals; the larval forms in a wide variety of rodents.

Geographic Distribution. T. mustelae is holarctic in distribution and has been reported from most of northern Eurasia and northern North America.

Host Occurrence. T. mustelae has been reported in the adult form from mink, weasels, and ferrets. It is probably limited to the Mustelidae. In the larval form, it has been found in many small rodents, and has experimentally infected others in which it has not been found naturally occurring (Table IV). I found T. mustelae only in C. gapperi.

Unidentified Larval Cestodes

Much of the larval cestode material was unidentified. Many of the cysts lacked hooks, and thus could not be identified even to genus. Other cysts had hooks which were not fully developed. The hooks were in most cases large, and resembled the hooks of the larger Taenia sp. It is probable that some of these hooks were T. rileyi. Others may be immature T. martis (Feder, 1803) which was first recorded from North America by Freeman (1956). Drawings of unidentified larval hooks are presented in Figs. 16 and 17.

The hooks of a larval cestode taken from Peromyscus maniculatus at location 4 on the Alaska Highway corresponded very closely in size and shape to those of Paruterina candelabraria (Goeze, 1782). They are shown in Fig. 18.

Nematoda

The Genus Rictularia Hall, 1916

The Genus Rictularia is widespread in North America and infects the Insectivora, Chiroptera, Rodentia, and Carnivora. The taxonomy of this genus is not clear and doubt exists as to the specific identity of many specimens.

Tiner (1948) divided the Rictularia parasitic in North American rodents into two groups; those with a transverse and dorsal oral opening and those with a roughly circular and anterior oral opening. Since the specimens collected in this study fall in the latter group, only members of this group will be considered here.

These include R. coloradensis Hall, 1916, R. onychomis Cuckler, 1934, R. ondatrae, Chandler, 1941, R. dipodomis Tiner, 1948, and R. microti McPherson and Tiner, 1952. McPherson and Tiner (1952) "consider that several additional species which are closely related to R. coloradensis occur in North America, and that maximum comb lengths, number of combs, and numbers of denticles are some of the characteristics that can be used to separate them into host specific groups."

Difficulties in specifically identifying members of the genus Rictularia arise for several reasons. One of the main characters seems to have been number of combs and spines. Yet often, in the region of the vulva, the transition from combs to spines is gradual. Usually the authors give no criteria for distinguishing between them. The total length of combs

and spines has also been used as a distinguishing feature but frequently no information is given as to how these measurements are to be taken. Males of this species are not abundant, so descriptions, when given, cannot take into account intraspecific variation. McPherson and Tiner observed two male R. coloradensis from a single Peromyscus leucopus (Rafinesque, 1818). One had no pre-cloacal fans and equal spicules (238μ); the other had three pre-cloacal fans and short unequal spicules (39μ and 88μ). Neither of these specimens agree with the description of male R. coloradensis as given by Hall, (1916) - which had no pre-cloacal fans and spicules 145 and 180μ long. The spicule lengths of parasitic nematodes are normally considered to be relatively constant, and valid criteria for specific determinations. Obviously this constancy does not apply to Rictularia. Sandground (1935) states "Too often . . . authors fail to indicate what they conceive to be the distinguishing characteristics of their species, . . . For the most part, specific descriptions are formulated on few specimens, since infections with Rictularia, as encountered in nature, seldom involve more than a meager number of worms. Hence the constancy of the characters used in specific diagnosis is assumed rather than demonstrated."

There seems to be no agreement on which characters should be used to designate species. Certainly so far as is known, number and size of pre-cloacal fans and condition of spicules in males are highly variable characters. The number of denticles, number of combs and spines, and length of combs and

spines seem at present to be the best characters. Some writers have indicated the importance of the position of the vulva, relative to the posterior end of the oesophagus, but Sandground (1935) and Gibbs (1957) considered this character to be subject to variation in R. affinis Jägerskiöld, 1909, at least. Gibbs (1957) in examining Rictularia sp. from Egyptian foxes found specimens which by the criteria of total length, egg size, total spine count, and vulvar fan of spines could be placed either in R. affinis or R. cahirensis Jägerskiöld, 1909. He analyzed these characters more carefully and from histograms and statistical analysis concluded that R. affinis, R. cahirensis, and R. splendida should be regarded as synonymous, and should retain the name R. affinis.

Thus we have at least one example of marked variation in a single species of Rictularia. Perhaps better series of Rictularia sp. from rodents will produce like results.

The Rictularia sp. recovered by me were identified to genus by the presence of their cuticular processes. Species identification was more difficult. Since only female worms were recovered, the descriptions of male worms were not used.

My specimens of Rictularia could be separated from R. ondatrae, R. dipodomis and R. onychomis on the basis of total numbers of cuticular processes. The following table presents data obtained from nematodes collected by me in comparison with the measurements of R. coloradensis and R. microti. In most respects, my material is closer to R. microti than to R. coloradensis (Table VII). McPherson and Tiner (1952)comment on

Table VII. Measurements of *Rictularia* spp.

	R. sp. Murray	*R. coloradensis* Tiner, 1935	*R. microti* McPherson and Tiner, 1952
Length (mm)	19.7 -28.2	15.8 -29.4	11.2 -27.8
Max. diameter ant. to vulva	.407- .618		.334- .465
Max. diameter post. to vulva	.629- .823		.494- .683
Buccal cavity - ant. ext. diameter	.065- .111		.052- .088
Buccal cavity - diameter of base	.0925- .148	.050- .073	.082- .094
Buccal cavity - depth	.074- .111	.053- .073	.062- .078
Oesophagus - length	2.64 - 3.70	1.78 - 3.44	2.9 - 3.5
Oesophagus - width at base	.111- .194		.117- .145
Vulva - distance from ant. end	3.24 - 4.16	1.67 - 3.14	3.75 - 4.82
Vulva - position relative to oesophagus	caudal	usually in front	caudal
Total no. cuticular processes	61-65?	60-64	64-66
No. cuticular processes ant. vulva	32-33	29-31	32-33
No. cuticular processes post. vulva	29-32?		31-33
No. cuticular processes at vulva	1		1
Max. comb length	0.120-0.166	.093- .122	.131- .145
Max. spine length	0.148-0.217		.150- .160
Egg size	27.3 x 32 - 46.0μ	32 x 45μ	22.8-29.1 x 39.1-58.1μ
No. denticles	19-24	15-17	24-25

the structural differences between the spines of R. microti and R. coloradensis. The spines of my specimens (Fig. 19) are morphologically very similar to those of R. microti as depicted by Tiner and McPherson. For these reasons my specimens have been assigned to R. microti. As more specimens from rodents become available, it may be found that the "forms" herein regarded as species are members of a highly polytypic species. Until such time, R. microti must be regarded as a valid species.

Life Cycle. The life cycle of R. microti is not known.

Geographic Distribution. R. microti has been reported only from St. Lawrence Island, and from the Brooks Range in Alaska. The present record, from the District of Mackenzie, is the most southern. It should perhaps be noted that R. coloradensis is a widespread, but seldom found, parasite of North American rodents.

Host Occurrence. R. microti has been reported from few hosts (Table IV). It is possible that R. microti is limited in occurrence to microtine rodents, but the scarcity of host records prohibits the drawing of a definite conclusion.

R. coloradensis, on the other hand (see Table IV) has been reported from a variety of rodent hosts. It is not strongly associated with the Microtinae and its most important affinities may lie with the Sciuridae.

The Genus *Syphacia* Seurat, 1916

Syphacia obvelata Seurat, 1916

All specimens of this genus corresponded to the description of *S. obvelata* (Rudolphi, 1802) as given by Hall (1916) and Hussey (1957).

Kruidenier et al. (1961) examined *S. peromysci* (Harkema, 1926) and *S. samoridini* (Erikson, 1938), two closely related species from *Peromyscus leucopus* and *P. maniculatus* respectively. Their objective was to determine whether these forms, from closely related hosts, were, in fact, good species. They found the nematodes sufficiently morphologically different to warrant the retention of both species.

I carried out a similar investigation on *Syphacia* spp. from *C. rutilus* and *C. gapperi*. The results are summarized in Table VIII. Mature specimens from *C. rutilus* were few, so the sample from *C. gapperi* was larger. It can be seen that the measurements from *C. rutilus* fit within those from *C. gapperi*. *En face* views of *Syphacia* sp. from the two hosts were indistinguishable. There is no reason to suspect that a different species of *Syphacia* infects each species of *Clethrionomys*.

Life Cycle. The life cycle of *S. obvelata* is direct.

Geographic Distribution. *S. obvelata* is cosmopolitan in distribution and has been reported from all over the world. Rausch and Tiner, 1949 showed that the parasite exhibits a pattern of localized abundance.

Table VIII. Measurements of S. obvelata from C. rutilus and C. gapperi.

	C. gapperi n = 20	C. rutilus n = 10
Total length	4.2 - 5.7 mm.	4.6 - 5.7 mm.
Greatest width	0.141 - 0.355	.148 - 0.325
Oesophagus		
length	0.222 - 0.359	0.251 - 0.351
width	0.033 - 0.067	0.037 - 0.056
Bulb		
length	0.082 - 0.111	0.091 - 0.111
width	0.093 - 0.111	0.093 - 0.103
Vulva - distance from ant. end	0.520 - 0.728	0.516 - 0.696
Egg size		
length	0.108 - 0.143	0.104 - 0.138
width	0.027 - 0.043	0.026 - 0.048

Host Specificity. Table IV indicates that S. obvelata is primarily a small rodent parasite. It, has, however been found in monkeys and man. I found the parasite in Clethrionomys rutilus, C. gapperi, and Synaptomys borealis (Richardson, 1828), the latter apparently constituting a new host record.

The Genus Protospirura Seurat, 1914

Protospirura muris (Zimmerman, 1780)

Specimens of the genus Protospirura were identified from the description given by Hall (1916). The specimens agreed with his figures in all particulars. An en face view of this species is pictured in Fig. 20.

No male specimens of any of the nematodes described were found. Many writers have commented on the relative scarcity of male nematodes. It is possible that males, being smaller, were overlooked during autopsy. Since gravid females were found in all species, it is obvious that males had been present. It may be that males of these species are short-lived and die and pass out of the host after copulation.

Life Cycle. The intermediate hosts of P. muris are mealworms, Tenebrio spp.(Hall, 1916).

Geographic Distribution. P. muris is holarctic in distribution and has been reported from widely separated areas. Rausch (1957) suggests that the occurrence of this nematode may be limited to boreal forest. To my knowledge it has not been reported from non-boreal localities.

Host Occurrence. P. muris seems to be limited to cricetid rodents and occurs most frequently in the Microtinae (Table IV). It is never abundant, and is usually found in only a few hosts. This probably accounts for its spotty distribution.

Comparison of the Parasites of Clethrionomys rutilus and C. gapperi

Parasite Species and Intensity of Infection.

The main purpose of this study has been to compare the endoparasitic fauna of C. rutilus and C. gapperi. This is best done with reference to Tables II, III and IV.

C. rutilus and C. gapperi which were taken from adjacent localities (Locations 6 and 7, Table III, only 12 miles apart) share as many parasite species (four) as do any two populations of C. gapperi; and more than do any two populations of C. rutilus. In addition, all of the parasites recovered from C. rutilus in this study were found in C. gapperi as well. Two parasites, Catenotaenia dendritica and Taenia mustelae, were found only in C. gapperi, but have been reported from C. rutilus by other authors (Rausch, 1951; 1952b) (Table IV).

A survey of the literature produced few examples of parasite species peculiar to either C. gapperi or C. rutilus (Table IV). The taxonomic status of Andrya primordialis, which has been reported only from C. gapperi, is uncertain (see p. 21). The other species limited in occurrence to C. gapperi, Cladotaenia globifera (Batsch, 1786), has only recently (Freeman, 1959) been well defined specifically, so little is known of its host occurrence. Both of these species, then, may well occur in C. rutilus as well as in C. gapperi.

Andrya arctica and Echinococcus multilocularis Leuckart, 1863 which have been reported from only C. rutilus , have

both been reported from other genera of microtine rodents (Lubinsky, 1959; Rausch, 1957). It is unlikely, then, that host specificity explains their occurrence in C. rutilus and absence in C. gapperi. E. multilocularis has been reported from only arctic regions where C. gapperi does not occur and probably would infect C. gapperi if its range is extended southward.

Most of the endoparasites of Clethrionomys spp. (Table IV) exhibit a wide host specificity and few, if any, are limited to the genus. It is unlikely, then, that any clear qualitative species difference exist

The average intensities of infection are given in Table II. The data show that there is no real difference in parasite load between C. rutilus and C. gapperi and it appears that the parasites of C. rutilus and C. gapperi are qualitatively and quantitatively much the same.

Total Numbers Parasitized; Age and Sex Differences.

There appears to be a significant difference in terms of total numbers parasitized between C. rutilus and C. gapperi (Table I).

A more detailed analysis of the data, in terms of age and sex of host, is presented in Tables IX and X. The adults of both species have approximately the same total infection rates and there seems to be no real difference in rate of infection between the sexes (Table IX). Table X indicates that the adults of both host species are infected to about the same

Table IX. Per cent infection rates of Clethrionomys spp. of different age and sex.

C. gapperi

	Male		Female		Both Sexes	
	n	% inf.	n	% inf.	n	% inf.
Adult	39	54	40	58	79	56
Juv.	54	35	35	49	89	40
Total	93	43	75	53	168	48

C. rutilus

	Male		Female		Both Sexes	
	n	% inf.	n	% inf.	n	% inf.
Adult	18	56	26	46	44	50
Juv.	50	12	53	6	103	9
Total	68	26	79	19	147	23

Table X. Per cent infection rates of adult and juvenile *Clethrionomys* spp. with each parasite.

Host	*C. rutilus*		*C. gapperi*	
Parasite	Adult No.=44	Juv. No.=103	Adult No.=79	Juv. No.=89
Andrya macrocephala	0	1	4	5
Catenotaenia dendritica	0	0	3	1
Hymenolepis horrida	35	8	34	30
Taenia mustelae	0	0	4	0
Taenia rileyi	9	0	3	0
Protospirura muris	2	0	1	1
Rictularia microti	16	0	0	1
Syphacia obvelata	9	0	15	16
Larval cestodes (unident.)	13	3	14	1

degree with nearly all the parasite species. The absence of A. macrocephala from adult C. rutilus and of R. microti from adult C. gapperi is, I think attributable to the relative scarcity of these parasites, rather than to host preference. Thus there seems to be no difference due to parasite species or sex of host between adult C. rutilus and C. gapperi.

The difference, then, in total numbers parasitized must be due to different rates of infection in the juvenile animals. Table X shows that immature C. rutilus of both sexes are much less heavily parasitized than immature C. gapperi.

The juveniles of both species are less heavily infected than the adults (Table IX), and the infection rates for individual parasite species are lower in juveniles than in adults in almost every case (Table X). Elton (1931) found that the rates of S. obvelata infections in immature wild Apodemus sylvaticus Linnaeus, 1758 were low, and rose steadily with age. Chan (1952) reported that, in experimental infections, young laboratory mice were more heavily infected than mature ones. I found no S. obvelata in immature C. rutilus but the infection rates for adult and juvenile C. gapperi were approximately equal. Only H. horrida and S. obvelata are sufficiently numerous to permit more detailed observations, which are summarized in Fig. 21. The proportion of hosts infected by these parasites varies considerably from location to location, and, in C. gapperi, S. obvelata and H. horrida may be more frequent in juveniles than in adults. Such is not the case with C. rutilus in which S. obvelata was never found in juvenile animals. The level of

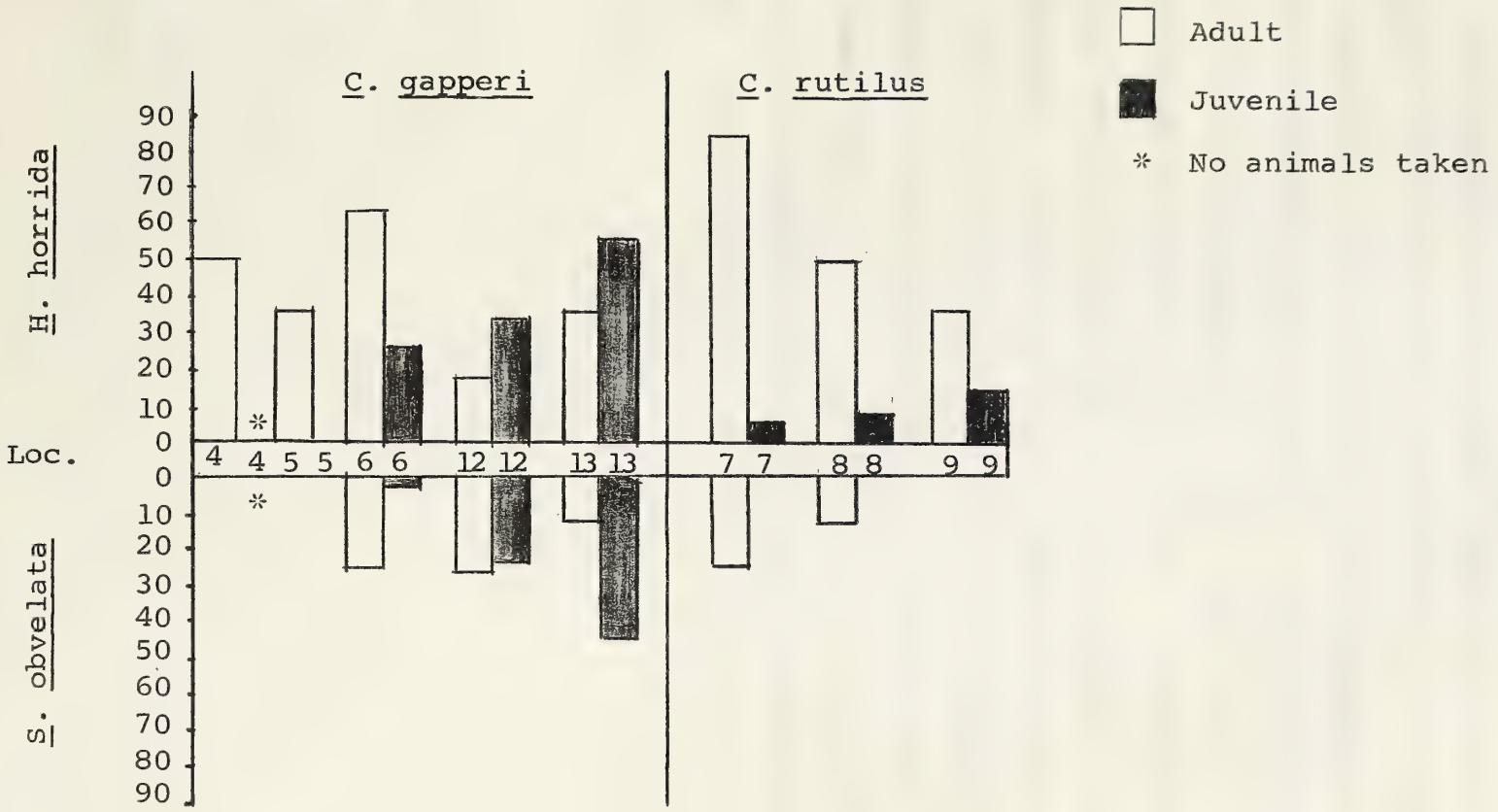


Figure 21. Per cent of adult and juvenile animals from eight locations infected with H. horrida and S. obvelata.

infection of H. horrida in juvenile C. rutilus is less than in adults from all three localities. (Young C. rutilus were always less heavily infected than young C. gapperi with the exception of C. gapperi from location 5.)

The reasons for the lower infectivity rate of juvenile C. rutilus cannot be stated with certainty. Perhaps C. rutilus are weaned at a later age than are C. gapperi, or their food habits during the early stages of their development may differ from those of C. gapperi in such a way so as to reduce the acquisition of parasite infections. It may be that young C. rutilus are more resistant to the parasites than are the young C. gapperi. If this is so, it appears that the resistance does not persist into maturity, since the percentage of infections in adults of the two species is, in most cases, approximately the same (Table IX). Chan (1958b) has reported that susceptibility to infection with S. obvelata varied with the strain of mouse. Such a phenomenon could be operating in the wild.

Comparison of the Parasites of *C. rutilus* and *C. gapperi* with those of *Microtus pennsylvanicus*, *Synaptomys borealis*, *Phenacomys intermedius*, and *Peromyscus maniculatus*.

All the parasites of *Clethrionomys* spp. found in this study except two (*C. dendritica* and *T. rileyi*) have been reported from *M. pennsylvanicus*, but the relative frequency of each parasite in the various hosts is hard to assess since records of infection rates are few. The present findings (Table II) suggest that *H. horrida* is not as common in *M. pennsylvanicus* as in *Clethrionomys* spp., but the paucity of *M. pennsylvanicus* autopsied in this study prohibits a definite statement. Rausch (1952b) considers *H. horrida* to be a boreal forest and subalpine species. If this is so, this cestode would be expected to be more frequent in *C. rutilus* and *C. gapperi* since these species are inhabitants of the boreal forest, while *M. pennsylvanicus* is typically an inhabitant of meadow and farmland. Although *M. pennsylvanicus* does occur in the boreal forest biome, it is restricted to open, marshy areas where the boreal overstory is sparse and grasses and shrubs are thick. *C. rutilus* and *C. gapperi* are found in the boreal forest proper. Most of the *M. pennsylvanicus* taken in this study, including the one from which *H. horrida* was recovered, were caught in the traplines which also yielded the *Clethrionomys*. I do not know whether *H. horrida* has ever been found in *M. pennsylvanicus* taken from grassland, but it is possible that ecological specificity rather

than host specificity is in evidence here. That is, the presence of H. horrida may not be so dependent upon the host species as upon the habitat occupied by the host species. Lubinsky (1957) reported H. horrida from M. pennsylvanicus in northern (boreal) Alberta, but did not find this cestode in M. pennsylvanicus from mid and southern Alberta. Records of H. horrida from a variety of hosts have come from many areas. The habitats of the hosts, were in most cases not given but I think it can be said that the majority of these hosts would be found in boreal and sub-alpine habitats, and certainly such habitats exist in all of the areas from which H. horrida has been reported.

Although S. obvelata was not recovered from M. pennsylvanicus in this study, Table IV suggests that this nematode is one of the vole's more common parasites. It is cosmopolitan in distribution, and in addition to the rodent hosts listed in Table IV it has been reported from monkeys and man (Yamaguti, 1961). It is probable that more autopsies would have revealed the presence of S. obvelata in M. pennsylvanicus in this study. This is likely true, as well, for the other parasites of Clethrionomys spp. recovered in this study which were not found in M. pennsylvanicus, but which have been reported from M. pennsylvanicus in the literature.

C. dendritica, to my knowledge, has never been reported from M. pennsylvanicus. If Wolfgang's definition of C. dendritica (p.) is accepted, this species has been reported from several families of rodent hosts (Table IV). Hence, host specificity cannot explain its absence from M. pennsylvanicus.

This parasite has also been reported from a variety of habitats and is not clearly associated with any one in particular. Hence, exclusion from M. pennsylvanicus by ecological specificity is unlikely. In short, there is no obvious reason for the absence of C. dendritica from M. pennsylvanicus. Rausch (1952b) states that "with possible local exceptions, it is not a common parasite of North American microtine rodents". The present study supports this contention, since only three of the 418 animals examined were infected with this parasite. It is possible that C. dendritica, though present in M. pennsylvanicus, has remained undetected because of its relative rarity in North America.

T. rileyi is the only other parasite recovered in this study from Clethrionomys spp. which has been reported from M. pennsylvanicus. As with C. dendritica, I do not think this means it never occurs in M. pennsylvanicus. Table IV illustrates that it has been found in cricetines as well as microtines, so intermediate host specificity does not seem to be operating here. Until the work of Riser (1956), the taxonomy of this species was not clearly defined, and misidentification may have prevented its having been reported from M. pennsylvanicus. The infection rate of intermediate hosts with T. rileyi may be naturally low. Only six animals in this study were infected, although at least some of the unidentified larval cestodes may have been this species. Presumably the final hosts (lynx, and coyotes) eat large numbers of rodents, and a relatively low infection in the prey species could maintain a high degree of infection in the predators.

Although M. pennsylvanicus shares most of the parasites of C. rutilus and C. gapperi, the former species is infected with several parasitic species which do not, apparently, infect the latter two (Table IV).

T. taeniaeformis (Batsch, 1786), not found in this study, has been reported from M. pennsylvanicus from several areas in north central United States. The final host of this parasite is the domestic cat, and feral house cats were present in the areas. The absence of this species in Clethrionomys may be explained by the absence of the final host, although it is not known whether T. taeniaeformis will infect Clethrionomys in any case.

Paranoplocephala infrequens and P. variabilis are important parasites of North American voles (Rausch, 1952b) although I have found no reference to their occurrence in Clethrionomys. They are found in several species of Microtus, including M. pennsylvanicus, over much of North America. Only P. variabilis was found in this study, but P. infrequens has been reported from M. pennsylvanicus in northern and central Alberta (Lubinsky, 1957). Since these cestodes are common parasites of Microtus spp., but have apparently not yet been reported from Clethrionomys, they may not be found in the latter.

Trematoda seem less important as parasites of Clethrionomys than of M. pennsylvanicus. Only Plagiorchis sp. has been reported from Clethrionomys, while several genera are known from M. pennsylvanicus. This is probably due to more frequent occurrence of M. pennsylvanicus in grassy, marshy habitat which

supports the molluscs serving as intermediate hosts for the trematodes.

The nematode fauna of M. pennsylvanicus (Table IV) is more varied than that of Clethrionomys, but I think it may be said that nematodes, in general, are not as frequent in microtines as are cestodes. With the exception of S. obvelata, the nematode parasites of microtines exhibit a spotty pattern of geographic distribution, and are almost always few in number in an individual infection. The taxonomy of microtine rodent nematodes is in many cases confused and often specific identification is not made, or if made, is not agreed upon by all workers. It is therefore difficult to assess host specificity in the nematodes of microtine rodents, and a large series of hosts from many areas is needed to elucidate the parasite-host relationships.

Very little can be said in comparing the endoparasitic fauna of P. intermedius and S. borealis with that of other microtine rodents. These microtines are rare, and their parasites are even less well known than those of other microtines, since the hosts themselves are so difficult to obtain in any number. The present study shows that P. intermedius is infected with Andrya macrocephala and S. borealis with S. obvelata (Table II). Both of these parasites are found in both species of Clethrionomys and in M. pennsylvanicus, and no host specificity is apparent.

The parasites of S. borealis and P. intermedius as reported in the literature are given in Table IV. None of these parasites are common to both species but all of them except H. polygyrus

(Dujardin, 1845) are shared by C. rutilus, C. gapperi, and/or M. pennsylvanicus. Here, again, there is a clear lack of host specificity. Larger series of P. intermedius and S. borealis will undoubtedly demonstrate even closer affinities between their parasites and those of the other microtine rodents herein considered, and may reveal parasites which are exclusive to Phenacomys and Synaptomys.

Rausch, 1957, considering nearctic microtine rodents at the generic level points out that "Dicrostonyx, Lemmus, Clethrionomys and Microtus are closely related phylogenetically, and their digestive tracts have become similarly adapted to a diet of relatively coarse, fibrous vegetation. They appear to fulfill more or less uniformly the habitat requirements of several species of helminths although there are a few which demonstrate a definite host-specificity".

A series of Peromyscus maniculatus examined in this study was very poor in parasitic fauna (Table IV). Only four individuals were infected, two with C. hepatica (Bancroft, 1893), two with an unidentified acanthocephalan larva, and one with a cestode larva which has been tentatively identified as Paruterina candelabraria (p.35). Of these, only C. hepatica has been reported from the other hosts collected, and this infection was experimentally induced (Table IV). All the Peromyscus but two were trapped in May and June in northern B.C. The extremely low infection rate may be attributed to the time of year. This question is more fully discussed in the following section.

Seasonal Variation

The rodent hosts autopsied in this study were collected from late May until mid September, 1962 and in early July, 1963. Since the animals were taken from widely separated areas whose seasonal changes do not strictly coicide, a detailed account of the seasonal variation in the parasitic fauna is neither possible nor justified. Some general comments, however, can be made.

From the end of May until June 22, 1962, 93 rodents were examined for parasites. These animals were taken at various points from mile 340 to 403 on the Alaska Highway in British Columbia. Of the total only 13 (15 per cent) harboured internal parasites. From mid July to mid September, 325 hosts were examined from Alberta and the N.W.T., and of these, 133 (41 per cent) were parasitized. The disparity is even greater if only the more frequently parasitized adults are considered. Thirteen out of 87 (15 per cent) of the May-June sample were parasitized, while of the July-September sample, 85 out of 133 (64 per cent) were parasitized.

The above data seem to illustrate that these voles are less heavily parasitized in the spring than they are later in summer and early fall. It is possible that the parasites were present in early stages of development, so small that they were overlooked during autopsy, in the May-June period. Even if this is true, infection must have occurred in the spring, and it is obvious that most microtines which overwinter are not heavily infected with parasites acquired during the preceding

summer. There are two possible reasons for this phenomenon - either most of the parasitized animals die during the winter, or the overwintering microtines lose their parasites before or during winter. It may be that both factors operate to some extent. It should be stated that none of the animals autopsied suffered any visible ill effects from the parasites infecting them. The intensity of infection of all the parasites (with the exception of S. obvelata in C. gapperi) was generally low, and even the occasional heavy infection with H. horrida did not visibly impair the health of the host. The average weights of infected and non-infected animals did not differ statistically ($df = 103$ $t = .497$ $p > .05$).

It is possible, however, that the parasites do have some effect upon their hosts, and that the onset of winter conditions increases its severity. Slight weaknesses caused by the parasite during the warm summer months when food is abundant may be sufficient to contribute to the death of the host, directly or indirectly, during cold weather when food is more scarce or during a period of physiological stress.

The reason or reasons for the loss of parasites prior to or during the winter are not well established. It may be that the winter diet of the host differs from the summer diet in such a way that the parasite is deprived of some essential nutrient, and thus cannot long survive. Reid (1942) and others have shown that even short periods of starvation will cause the loss of adult tapeworm infections. The life spans of most parasites are not known, but it is possible that some, at

least, live only a short time regardless of their environment. S. obvelata females mature and pass out of the host after 12 days (Chan, 1958a). The males of this species are voided after only six days (Chan, 1958b). Larval cestodes are usually present during the entire life of the host. Adult cestodes probably have a life span of not more than a few months. If the adult helminths do in fact have short life spans, then reinfection immediately after the loss of the parasites seems in some way to be prevented. The infective stages or the intermediate hosts (where involved) may not be available to the final host during the winter. On the other hand, a host which has just lost its endoparasitic fauna may have developed, during infection, an immunity which protects it from reinfection. The immunity could be short-lived, leaving the host susceptible to reinfection in the spring, or of long duration, in which case most of the infected animals taken during any one summer would be young of the year rather than animals which had overwintered. Since so few overwintering Clethrionomys were taken during this study, the data at hand shed no light upon this question. It is generally believed that most parasites which do not migrate through the hosts' tissue do not stimulate an effective immunity against subsequent infections. Since none of the adult parasites encountered in this study pass through the hosts' tissues, it is unlikely that an immune reaction would be responsible for the prevention of reinfection.

H. horrida and S. obvelata, the most common parasites of C. gapperi (see Table II) are not found in early June, but once

recovered, (22 June, H. horrida; 3 August, S. obvelata) they were present in all of the populations of C. gapperi examined during the remainder of the summer. No autopsies were performed from 22 June to 21 July 1962 but investigations in 1963 (4-14 July) at Lady Evelyn Falls showed that H. horrida and S. obvelata were both already present in high numbers. Since no autopsies were performed prior to July 4, nothing can be said of the spring occurrence of these parasites.

The data available seem to support the suggestion that the most important parasites of C. gapperi and C. rutilus (H. horrida and S. obvelata) are much reduced in numbers, if not entirely absent, during the early spring. The other parasites are too infrequent to permit any generalization concerning their seasonal abundance to be made.

It may be significant that S. obvelata was not found in the last three populations (locations 9, 10, 11, Table III) of C. rutilus to be examined, and that H. horrida was absent in the last two (Table III). Data available for S. obvelata (p.41) suggest that the parasite may normally exhibit a pattern of localized abundance and scarcity and the same could be true of H. horrida. This will be more fully discussed in the next section. S. obvelata was never common in the C. rutilus of this study, but H. horrida was found to be the most frequently occurring parasite of C. rutilus, and its absence from the above areas is surprising. If irregularity of geographic distribution is not accepted as the explanation for its absence, other reasons must be found.

I have earlier discussed the apparent absence of H. horrida from Clethrionomys populations in the early spring, and suggested the loss of parasites by the hosts in the winter months as a possible explanation. It could be that C. rutilus had already lost their H. horrida infections, and were not being reinfected. It should be pointed out that infections of H. horrida were found in 34 per cent of the adult C. rutilus and only 8 per cent of the immature animals. The populations of C. rutilus were composed largely of immature animals (31 of 42 at location 11; 8 of 11 at location 10) and H. horrida could have gone undetected because of the small size of the adult sample.

Population Cycles and Levels of Infection

Erickson (1944), with reference to snowshoe hares, has suggested that the endoparasitic load of a host population increases with the host population. That is, during years of low population densities, endoparasites are relatively scarce, and during years of high population densities, endoparasites are abundant. Bull (1962) reported that nematode infections may be high in dense rabbit populations, but that environmental factors may be more important than host density. My data have some bearing upon this theory in that three mouse populations seemed to have been in different population cycles. These populations were the 1962 and 1963 Lady Evelyn Falls population and the 1962 British Columbia population.

At Lady Evelyn Falls in the summer of 1962, Clethrionomys gapperi were numerous. In the summer of 1963 they were very scarce, and a drastic decline in the population had clearly occurred. Table XI summarizes the autopsy results from this area in the summers of 1962 and 1963.

It can be seen that instead of being less heavily infected at low population cycle (1963), C. gapperi was at least as heavily infected with its two most important parasites - H. horrida and S. obvelata.

Nothing definite can be said of the other parasites of C. gapperi, or of the other host-parasite relationships. The other parasites of C. gapperi are so infrequent that they may well have been at about the same level both years, but have gone undetected, especially in 1963 when only 17 C. gapperi

Table XI. Per cent of Lady Evelyn Falls specimens infected with each parasite species in 1962 and 1963.

Host	Number Autop.	Year	Parasite								
			A. macrocephala	*P. variabilis*	*T. rileyi*	*T. mustelae*	*S. obvelata*	*P. muris*	*R. microti*	*H. horrida*	Unid. larval cest.
C. gapperi	64	1962	-	-	3	5	27	2	2	44	3
	17	1963	6	-	-	-	29	-	-	47	12
M. pennsylvanicus	8	1962	-	13	-	-	-	-	-	-	14
	7	1963	-	-	-	-	-	-	-	14	-
S. borealis	1	1962	-	-	-	-	33	-	-	-	-
P. intermedius	1	1962	100	-	-	-	-	-	-	-	-
	6	1963	50	-	-	-	-	-	-	-	-

were taken. No larval cestodes were identified in 1963 because hooks were not found in any of the cysts. Most of the cysts were very small - perhaps since the autopsies were performed in early July in 1963 as opposed to early August in 1962. Some of the 1963 larval cestodes were probably T. rileyi and T. mustelae, and the total percentage of larval cestodes, identified and unidentified, for each year is almost the same (11 per cent in 1962; 12 per cent in 1963). It would appear then that the parasite load of C. gapperi is not dependent upon the density of the host population. Rausch and Tiner (1949) and Rausch (1950) have noted that there seems to be no increase of helminth parasites under high population densities in voles.

The 1962 British Columbia population was low and it is possible that a crash in rodent populations began there, and was not felt further east (Lady Evelyn Falls) until the following summer. The scarcity of parasites in the May-June British Columbia sample and the abundance of parasites in the July-September Alberta-Northwest Territories sample could therefore be interpreted as support for Erikson's theory. I think another explanation is more plausible.

All of the Clethrionomys taken in May and June were adults which had overwintered. The presence of lactating females proved that some young had been born, but they obviously had not left the nest. I think it is probable that few individuals survive the winter months, and the few that do, because of rapid reproduction, are able to produce a large population in

a short time. Thus a low mouse population in May and June may be the normal situation in any given area in the early spring, before the emergence of the first litter.

Too few autopsies of M. pennsylvanicus, S. borealis, and P. intermedius were made to permit comparisons between the two years. It is evident however, that while the population numbers of C. gapperi and C. rutilus fell markedly in 1963, those of S. borealis and P. intermedius seem to have risen. All four species were taken in the same traplines.

Geographic Distribution of Parasites

Table III and Figure 1 present data concerning the geographical distribution of parasites encountered in this study. In general, it can be said that most of the parasites of microtine rodents in this study are widely distributed over north western North America. Data from eastern North America are few, but the work of Schad (1954) in Quebec and Labrador strongly suggests that, on the whole, the same parasites are found in eastern North America. The more important parasites (H. horrida and S. obvelata) exhibit a relatively continuous pattern of distribution, and those of lesser importance are more irregularly distributed. Because of their relative rarity, they may be present in most populations, but remain undetected.

It is likely that the parasites which seem unimportant with regard to the host species as a whole may assume greater importance in localized host populations. R. microti and T. rileyi, which infected only 5 per cent and 2 per cent respectively, of the entire C. rutilus population were found almost exclusively in one location. Here, at Location 11, these values for infection rate were 12 and 10 per cent, respectively. Only adult animals were infected at this location and, considering adults only, the infection rates rise to 46 and 35 per cent. H. horrida was not recovered from any of the C. rutilus at Location 11. Thus, owing to irregular geographic distribution, the parasites which seem most important when considering the entire host species are sometimes less important than the "minor" parasites when a given geographic area is considered.

Intensive sampling of many areas is essential to the evaluation of the nature of any host-parasite relationship.

C. dendritica was found only in C. gapperi from Vega and Ministik Lake, Alberta and only in stands of almost pure aspen. However, the possibility that the occurrence of C. dendritica is limited to aspen stands is not supported by the data from the literature.

I can suggest no reason, other than insufficient sample size (11 individuals, 8 of which were immature), for the complete absence of endoparasites in C. rutilus from Location 10. This is the only area from which no endoparasites were obtained.

Multiple Infections

Five per cent of all hosts and 16 per cent of infected animals harboured two or more endoparasitic species. Hymenolepis horrida and Syphacia obvelata, the most common parasites, were found in the same host more often than any other pair of parasites. Statistical tests showed that actual frequency of occurrence of any parasitic pair was nearly the same as the predicted frequency of occurrence. Thus the presence of any one of the parasites considered does not seem to prevent subsequent infection with any of the others.

SUMMARY

The endoparasitic fauna of six cricetid rodents has been investigated. New host records are: Taenia rileyi and Rictularia microti from Clethrionomys gapperi and C. rutilus; Andrya macrocephala from Phenacomys intermedius; and Syphacia obvelata from Synaptomys borealis.

There was no difference, in terms of parasite fauna or intensity of infection, between C. rutilus and C. gapperi. Hymenolepis horrida and Syphacia obvelata were the most common parasites of adult C. rutilus and C. gapperi. Males and females of both species exhibited about the same rates of infection, but juveniles of both species were less heavily infected than were the adults. Juvenile C. rutilus were much less heavily infected than were juvenile C. gapperi. Infections with parasites other than H. horrida and S. obvelata were infrequent.

My data and data from the literature showed that the parasites of Microtus pennsylvanicus, Synaptomys borealis, and Phenacomys intermedius are similar to those of Clethrionomys spp., although M. pennsylvanicus harbours a number of parasites which apparently do not infect the other hosts.

Parasitic infections in all hosts were few in the spring, but became more frequent in the summer. The infected hosts may die, or else lose their infections during the fall and winter.

Host parasite data from the same area during high and low host population cycles indicated that the incidence of parasitic

infection does not increase with the host population, but remains relatively stable.

The more common parasites (H. horrida and S. obvelata) exhibited a fairly continuous distribution over the collection area. The other parasites, probably because of their relative rarity, exhibited a more spotty distribution.

Statistical tests showed that infection with any parasite does not inhibit infection with any other.

It is concluded that there is no species difference in the helminth parasites of Clethrionomys rutilus and C. gapperi.

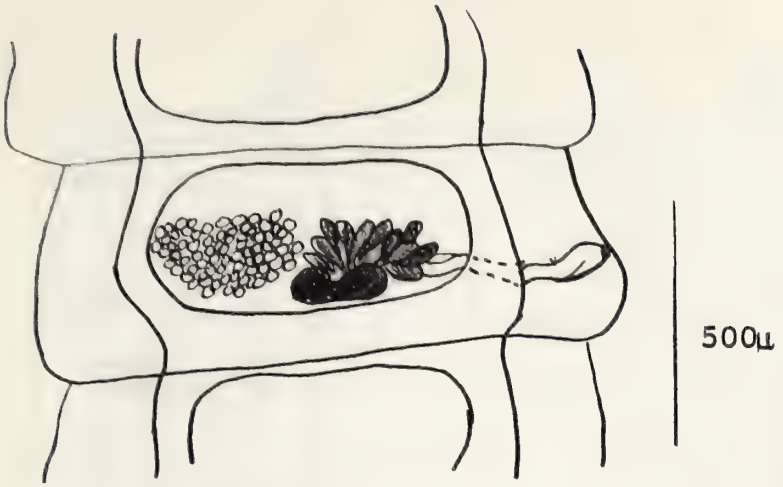


Figure 3

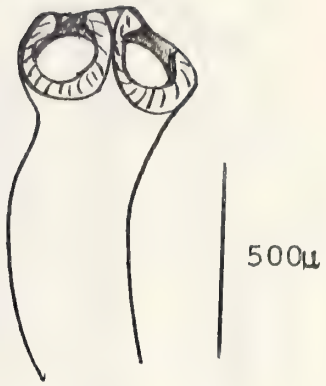


Figure 4

Figure 5

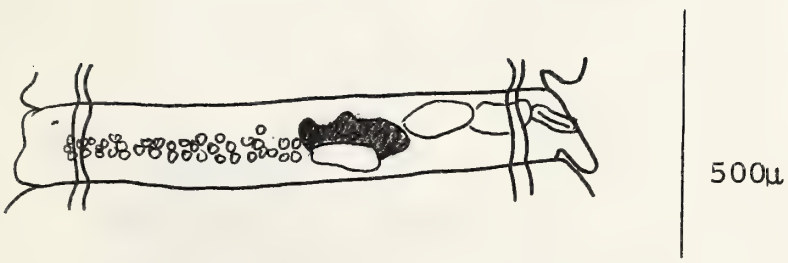


Figure 6

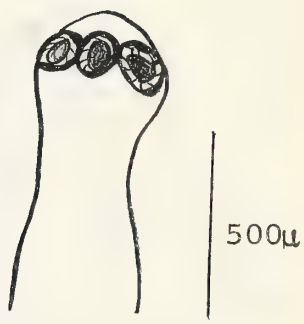


Figure 7

Figure 3. Mature segment of A. macrocephala
Figure 4, 5. Scolex of A. macrocephala
Figure 6. Mature segment of P. variabilis
Figure 7. Scolex of P. variabilis

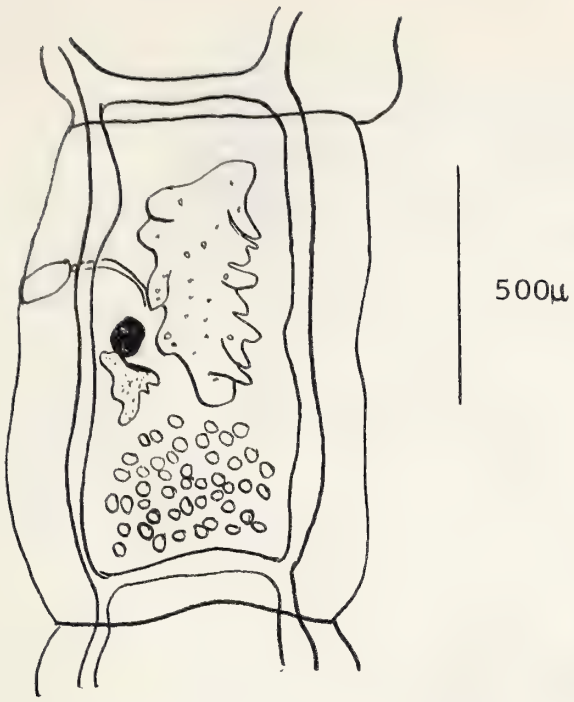


Figure 8

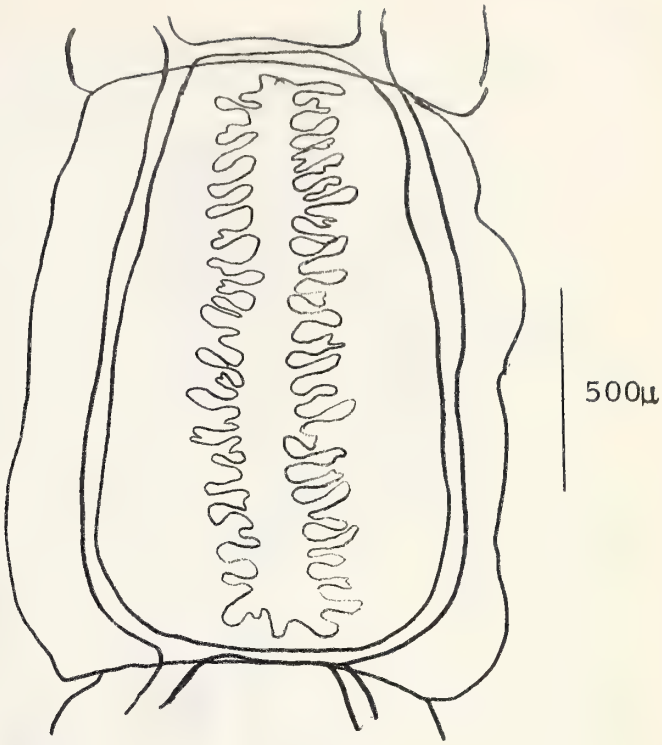


Figure 9

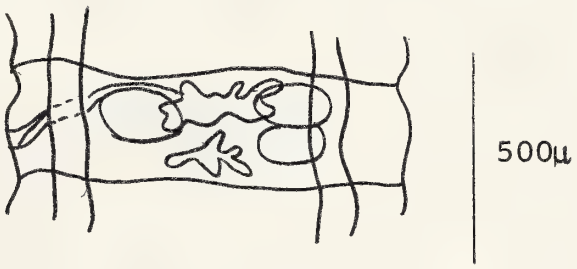
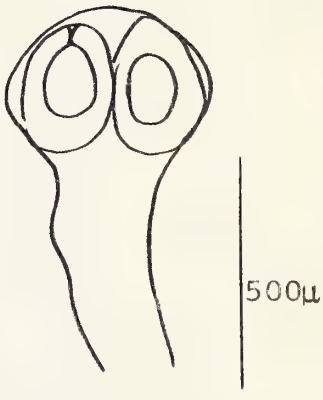


Figure 10



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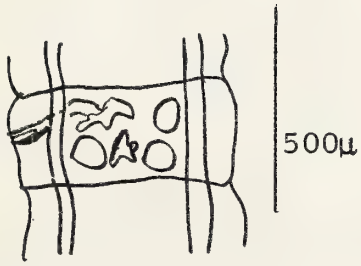

Figure 11

Figure 8. Mature segment of C. dendritica
Figure 9. Gravid segment of C. dendritica
Figure 10, 11. Mature segments of H. horrida
Figure 12. Scolex of H. horrida

Figure 13

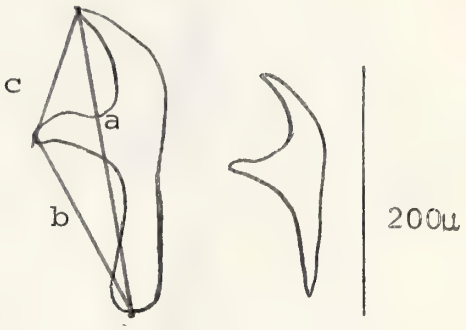

Figure 14

Figure 15

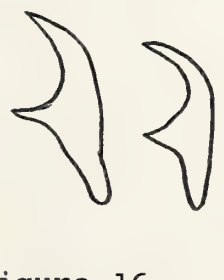

Figure 16

Figure 17

Figure 13. Scolex of H. horrida
Figure 14. Hooks of T. rileyi
Figure 15. Hooks of T. mustelae
Figure 16, 17. Unidentified larval cestode hooks

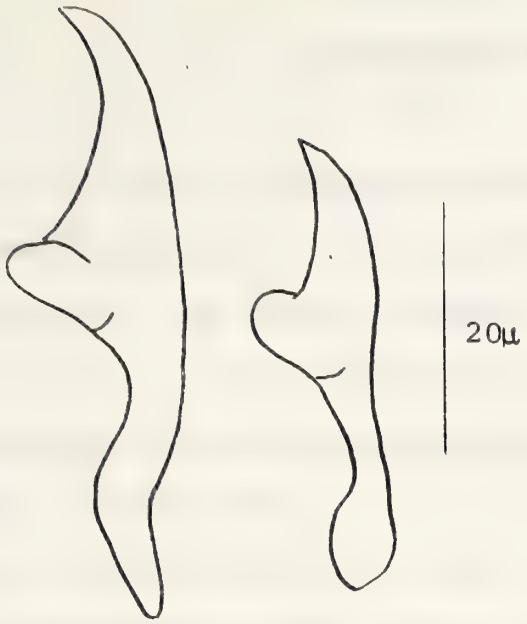

Figure 18

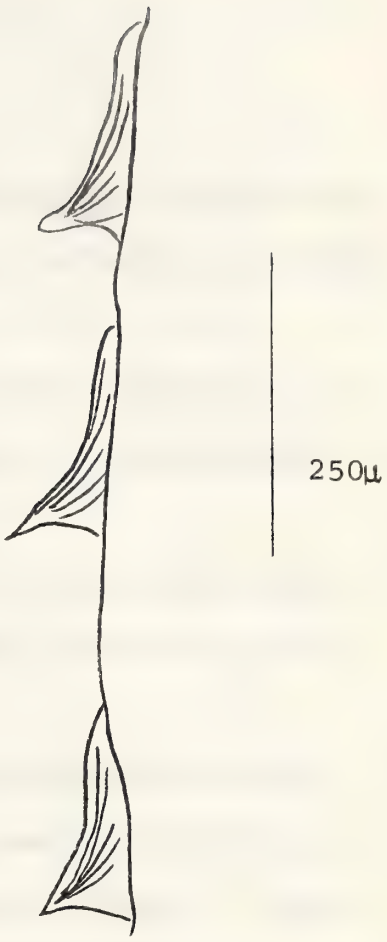

Figure 19

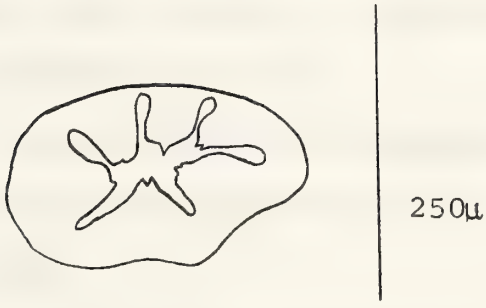

Figure 20

Figure 18. Hooks tentatively identified as P. candelabraria
Figure 19. Spines of R. microti
Figure 20. En face view of P. muris

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